typically occur seldom or not at all. This result does not fit to Sutcliffe and Pooles (1984) hypothesis on the initiating event/animal of TF.

At least some TF seem to be triggered by the estrus of the α-female, especially by the post-conception-estrus in mid-pregnancy. Kleiman (1979) also observed in *Leontopithecus rosalia rosalia* estrus related TF and parent-offspring-conflicts during mid-pregnancy (mid-pregnancy false estrus sensu Kleiman and Mack 1977).

As a whole there exists only a small bulk of data on TF in Callitrichidae and no information on the question whether we are right in assuming that siblings are even-ranking up to TF. Engel (1986) has shown that twins already reveal remarkable differences as to their social competence in early infancy. We do not know as yet however which event(s) or process(es) may be responsible for these differences in the relative position of the twins in the group hierarchy. This would mean that TF must have other and/or different function(s) as was hitherto believed. Up to now the published data on TF in marmosets and tamarins are too small for a sufficient explanation of the functional aspect of this behavioural phenomenon.

Acknowledgements

Zusammenfassung

Auftreten und Häufigkeit von Zwillingskämpfen beim Weißbüscheläffchen (Callithrix jacchus)

Zwillingskampf wurde in 32 von 39 Gruppen und in 27 von 83 Würfen des Weißbüscheläffchens *Callithrix jacchus* beobachtet. 39 Würfe waren heterosexuell, 23 isosexuell weiblich und 16 isosexuell männlich. Am häufigsten waren Zwillingskämpfe in reinen Männchen- (50 %) und isosexuellen Weibchenwürfen (46 %), am seltensten (17 %) unter heterosexuellen Wurfgeschwistern. Das Zwillingskampf-Alter betrug bei männlichen Wurfgeschwistern im Durchschnitt 188.5 Tage, bei weiblichen 241.7 Tage und bei heterosexuellen 237.1 Tage. Zwillingskämpfe waren über den gesamten Intergeburtenabstand des α-Weibchens verteilt, fünf zeigten eine zeitliche Beziehung zum 1. bzw. 2. postpartum-Östrus der Mutter. In 6 % aller Zwillingskämpfe mußte ein beteiligtes Tier aus der Gruppe entfernt werden, um schwere Verletzungen zu vermeiden.

Zwillingskämpfe konnten nur in Gruppen mit max. zehn Mitgliedern beobachtet werden, wobei ein relativ hoher Prozentsatz (37 %) in sehr kleinen Gruppen und in Abwesenheit gegengeschlechtlicher Gruppenmitglieder (Eltern ausgenommen) zu verzeichnen war.

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Homing behavior of Wood mice *(Apodemus)* in a geomagnetic anomaly

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Abstract

Experiments have been performed to test the hypothesis that a previously described local directional bias in the homing behavior of wild mice resulted from an interference between homeward orientation and a tendency to go up the gradient of magnetic intensity at the site of a weak geomagnetic anomaly. An analysis of homing success of 440 European woodmice (*Apodemus flavicollis* and *A. sylvaticus*) tested at any of four sites affected by the same magnetic anomaly provides only limited support to the hypothesis. The results point to the possibility that a stronger effect of the anomaly could be a drop in homing success in the immediate surroundings of the magnetic trough of the anomaly.

Introduction

In the early 1960's, one of us carried out a homing experiment near Lausanne, Switzerland, with European wood mice (*Apodemus sylvaticus* and *A. flavicollis*), in which animals displaced from different cardinal directions had different homing performances (Bovet 1962). Using the terminology of the time, he described the differential pattern as a directional effect (= Richtungseffekt) (e.g. Kramer et al. 1956, 1958; Pratt and Wallraff 1958). Subsequently, we learned from a paper by Meyer de Stadelhofen et al. (1973) that Bovet's (1962) research area was located in the Jorat magnetic anomaly (see Fig. 1,A). In the mean time, evidence had been accumulating on the role of magnetic cues in bird orientation (reviewed by Keeton 1974). This led us to perform, in 1975–1977, the series of experiments reported in this paper to evaluate the possibility that the directional effect described by Bovet (1962) was linked to the magnetic anomaly, and that natural magnetic cues could affect the orientation of mice. The results obtained were not clearly interpretable in terms of a magnetic effect at this time and were filed away.

Since then, experiments with pigeons have led to a better characterization of how and when their homing orientation and/or performance is affected after release in various kinds of magnetic anomalies (review in Wagner 1983). On the other hand, several experiments have been performed with rodents, some of which suggest an important role of magnetic cues in the homing orientation of these animals (Mather and Baker 1981; August 1985), others not (Etienne et al. 1985, 1986). These recent developments on the role of magnetic cues in the spatial orientation of higher vertebrates prompted the present re-examination of the results of the 1975–1977 experiments.

The Jorat magnetic anomaly, a part of which is shown in Fig. 1, comprises a fairly uniform disruption of the normal pattern of gradients of total magnetic field intensity, that affects an area of roughly 50 × 35 km (Meyer de Stadelhofen et al. 1973). Bovet's (1962) major basis for assuming a directional effect was that in the area he worked in (around A in Fig. 1), the homing success (= ratio of number of successful homers to number of animals tested) was highest for animals which had to travel up to 1 km South in order to home, null for animals which had to travel toward North, and intermediate
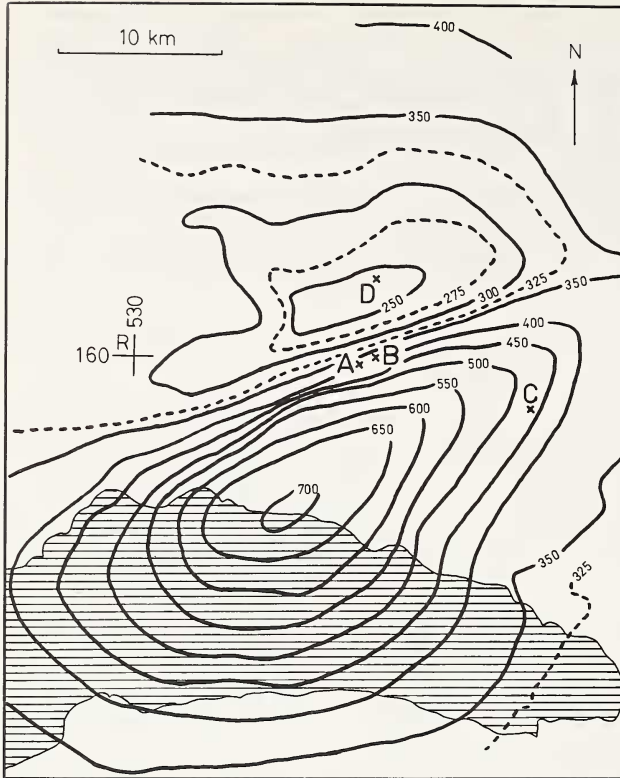
Fig. 1. Map of the Jorat magnetic anomaly. Numbers on isodynamic lines indicate total magnetic intensity at ground level (in nT, +46 000). A, B, C, D are the central points of the four experimental areas. R is point 530,000/160,000 of the Swiss reference grid system. Stripped area is part of Lake of Geneva. (Redrawn from MEYER DE STADELHOFEN et al. 1973, with permission)

toward East and West, with slightly higher figures toward East than West (Fig. 2). Considering that the magnetic isopleths in the area around A run along an ENE-WSW axis and the gradient goes up toward SSE (Fig. 1), we hypothesized that, in addition to a homeward tendency, the mice may have a tendency to go up the abnormally steep magnetic gradient (i.e., about 70 nT/km vs. about 10 nT/km in normal conditions, at ground level). The convergence of the two tendencies should facilitate homing, whereas their divergence should impair it. This would account not only for the strong difference between South and North and the intermediate values for East and West, but also for the small difference between East and West: animals homing toward East go slightly up the gradient; animals homing toward West go slightly down the gradient. Our 1975–1977 experiments were then aimed at testing the following predictions of the hypothesis with respect to homing success:

1. New displacements performed in the area around A should reveal the same directional effect as in 1962.
2. Displacements performed in an area such as that around B (Fig. 1), where the magnetic isopleths have the same orientation and the gradient goes up in the same direction as in the area around A, should reveal the same directional effect.
3. Displacements performed in an area such as that around C (Fig. 1) where the magnetic isopleths are oriented NNE-SSW and the gradient goes up toward WNW, should reveal a directional difference such that homing success toward West is high, toward East low, and toward North and South intermediate with a small advantage for North.
4. Displacements performed in an area like that around D (Fig. 1), which is in a magnetic trough, should not reveal any directional difference.

The hypothesis and its predictions were based on the 1962 experiment and on the description of the anomaly by MEYER DE STADELHOFEN et al. (1973), with no specific input from other sources. However, during the tests, they received support from a paper by FREI and WAGNER (1976). These authors reported then that homing pigeons released at various sites within the very same Jorat magnetic anomaly had an initial orientation which was a

compromise between homeward orientation and a tendency to fly up the magnetic gradient, thus something very similar to our hypothesis. On the other hand, the evidence eventually produced by Mather (1985) suggests that the magnetic deposits found in the head of woodmice make them potentially as sensitive to magnetic cues as, for instance, pigeons. According to Gould (1982), behavioral evidence suggests this sensitivity to be at least 10–30 nT in pigeons; also, the single domains of magnetite discovered in pigeons could produce a resolution better than 1 nT. Taken together, these data suggest that, along the steepest slope of the gradient in the Jorat magnetic anomaly, woodmice could detect differences in field strength over distances of the order of 200 m or less. Our hypothesis was, therefore, not unreasonable in this respect.

Material and methods

The experiments were performed in four areas centered around points A, B, C, and D shown on Fig. 1. Grid references according to Carte nationale de la Suisse (1 : 25 000) are: A = 543,900/159,800; B = 544,850/ 160,280; C = 554,600/157,300; D = 544,800/165,500.

Fig. 2. Results of the 1962 experiment: homing success obtained at various stations around release site A (see Fig. 1), in percent of animals that homed. Numbers in boxes indicate numbers of animals displaced. S, E, W, N correspond to direction of home site, as seen from A. 500 and 1000 are distances (in m) from release site to home site. Vertical arrows point to zero values. Difference in homing success between South and North was nearly significant at 500 m, and significant at 1000 m (p = 0.094 and p = 0.019, respectively; Fisher's exact probability test, one-tailed). Concordance between the two distance conditions for a decrease of homing success figures in the order S-E-W-N was nearly significant: Spearman's rs = 0.95)

The point of lowest magnetic intensity recorded by Meyer de Stadelhofen et al. (1973) within the contour of the 46 250 nT isopleth is located 1200 m ESE of D (their station 172: 46 238 nT).

In each area, a number of trapping stations were established according to a symmetrical pattern around the central point. Each station had 20 home-made single catch live-traps, on 4 rows of 5 traps forming a grid of 10 × 10 m squares. We tried to find areas as large as possible that would be at an appropriate location with respect to geomagnetic characteristics, and would cover homogeneous habitat. It is extremely difficult to find large areas of homogeneous habitat in a densely populated country like Switzerland, and we had to content ourselves with areas that were essentially "wooded" (with a variety of deciduous and coniferous species), with no major clearings. Around A and B, we could place 12 stations each, at 250, 500, and 750 m North, East, South and West of the central point. Around C, we could place only 8 stations, at 250 and 500 m North, East, South, and West of the central point. Around D, we were limited to 6 stations at 250, 500 and 750 m South and North of the central point. In any one area, all the stations were operated similarly and simultaneously. Details on trapping operations are shown in the Table. All the traps were checked every morning after a night of operation.

All the mice were marked at first capture with numbered ear-tags and with toe-clips. Only mice considered as residents of a home range overlapping a single trapping station were used in the experiments. Criteria for residency were that a mouse should have been captured at least three times on at least five consecutive calendar days, and should have been always captured at the same station. All the mice used in a given area were displaced and released at the central point of that area, at places marked A, B, C, and D in Fig. 1. Displacements were performed by transporting the mice on foot and by car in individual jars without view of the surroundings. Routes followed during displacement resulted from a compromise between avoiding long detours for the mice and allowing the trapper(s) to complete trap checking between sunrise and noon at the latest. All displacements were followed by release on the same day.

Depending on when a given mouse was displaced, traps were available for recapture at the home station a variable number of nights. For the last displaced mouse in any area, traps were available for at least 5 nights after release, spread over at least 7 calendar days. There was no obvious natural barrier between any home site and the corresponding release site. All the occasional rivulets and creeks were of a type passable by mice (Bovet 1965). The only two-lane paved road that went between several home sites and release sites (in areas A and B) was of a type passable by mice (Kozel and Fleharty 1979) and was actually crossed by several successful homers (which could not have homed without doing so).
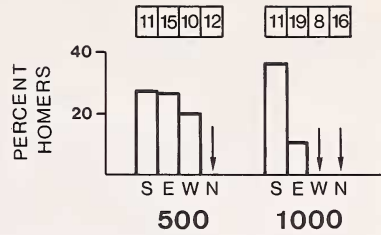
Trapping schedules. (Dates formated D.M.Y.)

Area	Number of stations	Begin of trapping	First displacement	Last displacement	End of trapping	Number of nights of trapping	Number of mice displaced
A	12	16. 10. 75	22. 10. 75	7. 11. 75	21. 11. 75	22	93
B	12	9. 8. 75	14. 8. 75	3. 10. 75	11. 10. 75	42	151
C	8	6. 4. 76	21. 4. 76	11. 6. 76	19. 6. 76	49	141[a]
C	8	12. 8. 77	25. 8. 77	6. 10. 77	13. 10. 77	43	
D	6	25. 10. 77	3. 11. 77	10. 11. 77	25. 11. 77	18	55

[a] 1976 and 1977 pooled for area C.

The experiments involved 440 *Apodemus*, each used only once. Numbers of mice studied in any one area are shown in the Table. Of these, 245 (145 ♂♂ and 100 ♀♀) were identified as *A. flavicollis*, and 174 (98 ♂♂ and 76 ♀♀) as *A. sylvaticus*. The remaining 21 mice (10 ♂♂ and 11 ♀♀) could not be attributed safely to either species, due to "intermediate" field identification characters. For the analysis of results, all 440 mice were pooled, irrespective of the species they belonged to. According to MERMOD (1969), home range sizes are similar in the two species, which, as a rule, implies similar homing performances (see ANDERSON et al. 1977; BOVET 1978).

Source for statistical tests was SIEGEL (1956).

Results

Homing success values obtained at any one trapping station are shown in Fig. 3. Due to the well known depressing effect that displacement distance has on homing success (BOVET 1978), comparisons related to our magnetic hypothesis can be meaningfully made only
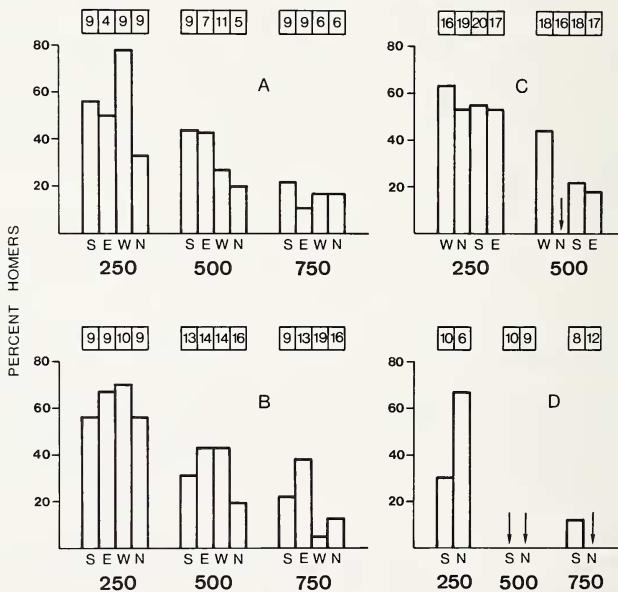

Fig. 3. Homing success obtained at the various stations in areas A, B, C, and D, in percent of animals that homed. Numbers in boxes indicate numbers of animals displaced. S, E, W, N correspond to direction of home site, as seen from release site. 250, 500, 750 are distances (in m) from release site to home site. Vertical arrows point to zero values

among stations that are at the same distance from the release site. An analysis of the relationships between homing success and distance in areas A and B has been published elsewhere (Bovet 1982).

Areas around A, B, or C

For each displacement distance in any area around A, B, or C, the four histogram columns displayed in Fig. 3 are arranged in descending order based on the predictions of the hypothesis. Of the 48 possible comparisons between any two values obtained in the same area and over the same distance, only three reveal a significant difference at the 0.05 level (χ^2 or Fisher's exact probability test, one-tailed): area B, 750 m, E > W; area C, 500 m, W > N, and W > E. If, in an attempt to overcome the effect of small sample sizes, we pool the comparable values obtained around A, B, and C (i.e., all results obtained over a given distance in directions corresponding to expected highest, second highest, third highest or lowest levels, respectively), the statistical results remain essentially the same. A significant difference is found in only two cases out of 18: 500 m, expected highest > expected lowest; and 750 m, expected second highest > expected third highest. It is thus obvious that, at this level of analysis, the statistics do not confirm the predictions of the hypothesis. There is however a trend, apparent in Fig. 3, for homing success to be higher in those circumstances where the hypothesis predicts it to be higher. Considering values that correspond to expected highest and lowest levels in any set of comparable figures (S vs. N around A or B, W vs. E around C), a sign-test shows the former to be significantly more often the highest of the two than expected by chance ($N = 7$; $x = 0$; $p = 0.008$). If we give up the rather stringent prediction of a consistent difference between expected second and third highest levels and we pool these two into a single "intermediate" level, there is a significant concordance among the experimental conditions for a decrease of homing success from expected highest through intermediate to lowest levels (Kendall coefficient of concordance; $N = 3$, $k = 8$, $s = 51.5$; $p < 0.05$).

Area around D

There is no significant difference in homing success between South and North over the three distances tested. Although this fits the prediction of the hypothesis, it has no real supporting value because the similar analysis applied to the other areas does not verify the contrasting predictions. Not predicted by the hypothesis, homing success over any one distance was steadily lower around D than around either A, B, or C (all directions pooled). The differences were particularly strong over 500 m ($D < A$: $p < 0.01$; $D < B$: $p < 0.01$; $D < C$: $p < 0.05$). This difference between area D and the other areas cannot be related to any obvious topographical or vegetational feature, nor to a matter of time of year when the experiments were carried out (compare A and D, Table).

Discussion

The results of this study provide limited support of the hypothesis that the homing performance of *Apodemus* was facilitated in certain directions and impaired in others as an effect of the magnetic anomaly. We did find evidence for a pattern of directional differences in homing success that coarsely fits the predictions of the hypothesis, but these differences were of very low amplitude and affected the overall homing performance in a marginal way only. On the other hand, the results indicate that the absence of a directional gradient of magnetic intensity in the trough of the anomaly (around D) might impede homing performance in mice.

The marginal effect of the anomaly on the homing performance in areas A, B, and C

seems to contradict the claims of Mather and Baker (1981) or August (1985) to the effect that woodmice *(Apodemus sylvaticus)* or white-footed mice *(Peromyscus leucopus)* are strongly disoriented after displacement in a disturbed magnetic field. The contradiction is apparent only. In Mather and Baker's (1981) as well as in August's (1985) experiments, the magnetic field was altered only during displacement, and returned to normal before release. By contrast, in our experiments, the "alteration" of the field was steady during both displacement and homing trip, a condition that did not affect the homing performance of hamsters in an arena (Etienne et al. 1985, 1986). Also, due to the size of the Jorat anomaly, it can safely be assumed that all our mice had spent their whole life within it. Considering current models of the ontogenetic development of navigational abilities in free-ranging animals (e.g., Wiltschko and Wiltschko 1982; Baker 1984), it can be argued that the features of the magnetic anomaly were normal indeed to our mice and that the animals were tested in an "undisturbed" magnetic field. Furthermore, the magnetic changes produced experimentally by Mather and Baker (1981) and by August (1985) were claimed to act directly on the homeward orientation process of the mice, while the limited effect documented in this study seems to result from the interference of a tendency to go up a magnetic gradient with an otherwise normal homeward orientation process. This part of our results, therefore, pertains to Mather and Baker's (1981) or to August's (1985) findings only in as far as it suggests, however elusively, that magnetic cues can affect spatial orientation in wild mice. For the rest, it neither supports nor infirms these authors' conclusions. Similarly, and for the same reasons, our results provide no other element in the argument developed in recent years as to whether or not humans use magnetic cues for their homeward orientation (Baker 1981; Gould and Able 1981; Fidles et al. 1984; Westby and Partridge 1986). On the other hand, the overall low homing performance that we observed in the magnetic trough is more consistent with the conclusions of Mather and Baker (1981) and of August (1985) that mice use magnetic cues as a basis for route-based navigation. However, several replications of the observation should be made before the possibility can be excluded that the effect was due to non-magnetic, local factors.

During the last decade, several experiments have been performed on the homing behavior of pigeons released in geomagnetic anomalies (e.g. Frei and Wagner 1976; Wagner 1976; Walcott 1978; Frei 1982; Kiepenheuer 1982; Lednor and Walcott 1983; for a review, see Wagner 1983). Besides the species used, there are a number of basic differences between these experiments and those reported in the present paper. Most pigeons experiments were performed in "strong" anomalies the geophysical effects of which are more intense than in the Jorat anomaly at ground level, but extend over a much smaller area, and result in a chaotic local pattern of magnetic intensities. They were usually performed with "experienced" animals, thus likely to use location-based systems of orientation, by contrast to our fully "naive" mice, that were more likely to use route-based systems (see Wiltschko and Wiltschko 1982; Baker 1984). Finally, they involved the displacement of pigeons from outside the anomaly into it. Because of these fundamental differences in procedures, any attempt to compare the results of these studies with ours appears to be pointless. However, some of the experiments reported by Frei and Wagner (1976) are much more related to ours. Besides being performed in the same, weak magnetic anomaly, they involved pigeons that were little trained and/or that had both their home site and their release site in the anomaly. As mentionned in the introduction, Frei and Wagner's (1976) results suggest an effect essentially similar to our effect, i.e., a compromise between homeward orientation and a tendency to move up the magnetic gradient. The effect in pigeons, measured on the distribution of individual bearings at various times between release and vanishing, was more pronounced close to the release site (presumably a few hundred meters, i.e., the range on which we measured it in mice) than farther away (up to 3 km). Eventually, Frei (1982) reported on additional experiments in the same